PAN-PACIFIC ENTOMOLOGIST
73(3): 172–183, (1997)

FORAGING ACTIVITY, TRAILS, FOOD SOURCES AND PREDATORS OF *FORMICA OBSCURIPES* FOREL (HYMENOPTERA: FORMICIDAE) AT HIGH ALTITUDE IN COLORADO

JOHN R. CONWAY
Department of Biology, University of Scranton,
Scranton, Pennsylvania 18510

Abstract.—The thatching ant, *Formica obscuripes* Forel, was studied at high altitude in Colorado by marking workers and flagging trails. Mounds had 1–5 trails up to 53.6 m long. Seventeen mounds had trails going to a Douglas fir tree (*Pseudotsuga* sp.). Activity at trail checkpoints varied from 0–171 ants per minute during the day. Ants marked on one mound were found on as many as 24 other mounds up to 77.9 m away. Ants were observed on 12 plant species and tended aphids on nine of them. Leaf clusters on mountain snowberry (*Symphoricarpos rotundifolius* A. Gray) and Saskatoon serviceberry (*Amelanchier alnifolia* Nuttall) contained up to 1163 aphids/cluster and predaceous insect larvae. Ants also tended treehoppers, scale insects, mealybugs and galls on plants. Ants were seen feeding on an owl carcass, but usually scavenged dead insects. A bear cub was observed excavating mounds. The results are compared to other studies of this species.

Key Words.—Insecta, *Formica obscuripes*, thatching ant, Colorado, foraging, trails.

Formica obscuripes Forel, is a species of the *Formica rufa* group (Weber 1935) that ranges from northern Indiana and Michigan westward across the United States and southern Canada. It is an abundant ant in western North America, especially in semi-arid sagebrush areas and has been found at altitudes up to 3,170 m in Nevada (Wheeler & Wheeler 1986) and 2,896 m in Colorado (Gregg 1963).

My study compared *F. obscuripes* predation, trails, foraging activity, and food sources at high altitude in Colorado with studies in other areas (McCook 1884; Jones 1929; Cole 1932; Weber 1935; King & Sallee 1953, 1956; Talbot 1959; 1972; Gregg 1963; Kannowski 1963; Windsor 1964; Bradley 1972, 1973a, 1973b; Clark & Comanor 1972; Knowlton 1975; Herbers 1977, 1978, 1979a, 1979b; Inouye & Taylor 1979; Wheeler & Wheeler 1983, 1986; Henderson & Akre 1986; O'Neill 1988; Seibert 1992; McIver & Loomis 1993; McIver & Steen 1994).

MATERIALS AND METHODS

The study site was in Gunnison County, Colorado, N of Blue Mesa Reservoir and W of Soap Creek road (N 38 30.350′, W 107 19.602′) at an altitude of 2560 m. Field observations were conducted from 5–6 Aug 1990; 20 Jun–11 Oct 1992; 28 Jun–16 Aug 1993; 29 Jun–31 Jul and 14–16 Aug 1994; 3, 29–31 Jul and 15–16 Aug 1995, and 1–4, 18–19 Aug 1996. Eighty-five mounds were mapped in a study area (64.6 m × 114 m) using a surveyor's transect and compass. The area, dominated by big sagebrush (*Artemesia tridentata* Nuttall), is adjacent to a quaking aspen grove (*Populus tremuloides* Michaux). Other plants in the study area were *Chrysothamnus nauseosus* (Pallas) Britton (rubber rabbitbrush), *Purshia tridentata* (Pursh) De Candolle (antelope bitterbrush), *Lupinus argenteus* Pursh (silvery lupine), *Symphoricarpos rotundifolius* A. Gray (mountain snowberry), *Rosa woodsii* Lindley (Woods rose), *Urtica gracilis* Aiton (stinging nettle), *Penstemon*

strictus Bentham (Mancos penstemon), *Ipomopsis aggregata* (Pursh) Grant ssp. *aggregata* (trumpet gilia), one Saskatoon serviceberry tree, *Amelanchier alnifolia* var. *pumila*, and one Douglas fir tree, *Pseudotsuga* sp.

Hundreds of workers were individually marked on eight mounds and five plants in 1992–1993 with a fine-tipped brush and model airplane paint. Thousands more were marked by spraying five mounds in 1994 and one mound in 1996 with acrylic enamel. These marking techniques did not seem to adversely affect many workers (O'Neill 1988). Trails were delineated with sprinkler flags. The terms "nest" and "mound" are used synonymously.

RESULTS

Carnivorous, Insectivorous, and Herbivorous Habits.—Although workers were observed feeding on a small owl carcass on 6–8 Jul 1993, they usually scavenged dead arthropods from late June to October. Beetles were common prey. Workers occasionally attacked and carried live insects, but did not pursue some observed on their mounds, such as aphids, a mealybug, a beetle, a spider, and another ant species.

Workers were seen with plant material at three mounds: a sagebrush leaf, a sagebrush gall, and a red flower.

Predation.—Seventeen mounds were found disturbed or excavated in the summers of 1993–1995. On 6 Jul 1993, a bear cub was observed digging about 25 cm into one mound and about 15 cm into another mound, presumably feeding on workers and brood. Nests recovered and one mound was largely rebuilt two weeks later.

Trails.—Well-defined trails lead from mounds to plants and/or to other mounds. Workers carried twigs, insects and spiders, nestmates, callows, wingless queens, larvae, and pupae on the trails.

Each of the mounds studied (n = 10) had 1–5 main trails. Three mounds had branching trails: two mounds had a single branch off a trail; the third mound had two branching trails. Trails (n = 35) from these mounds ranged from 0.6–44.8 m long (mean = 7.1 m). The greatest decline in trail number for a mound over the years was from four in 1992 to one in 1994. The mound was abandoned in 1995.

Marking Experiments.—Marking experiments and trails suggest that some mounds are related. Mounds #8 and #9 were connected by a trail and workers marked on mound #9 were found on mound #8. A trail ran between mounds #80 and #81 and workers marked on each mound were found on both. In addition, workers marked on a nearby Saskatoon serviceberry appeared on both mounds and both mounds had trails to the same sagebrush.

Workers marked on a particular mound were found on vegetation and other mounds. For example, mound #9 workers were found on nine mounds 4.3–14.6 m away and on vegetation up to 8.2 m away.

Circadian Activity.—Workers were seen leaving mounds as early as 06:40 and as late as 20:45 h in June 1992, but mound activity fluctuated greatly during the day. Mounds were active from 07:48 to approximately 11:00 h from 1 Jul–16 Aug 1993, although activity sometimes subsided as early as 10:45 and sometimes not until noon. Mound activity increased again from 13:45 to 18:40 h. It was not

determined if mound activity was related to changes in temperature, sunlight, or other environmental factors.

Trail activity also changed during the day. Ant activity monitored for seven days in July 1994 at four checkpoints along two trails to the Douglas fir, fluctuated from 0–171 ants/min. Trail activity at the checkpoints was generally high in the morning from 07:31–11:17 h, but declined from 10:12–17:05 h. Activity increased and was high again later in the day from 17:07–18:59 h. At three of four checkpoints, the highest trail counts (165–171 ants/min) occurred from 17:17–18:07 h. The highest count at the fourth checkpoint (117 ants/min) occurred in the morning at 09:03 h.

Trails to Douglas fir.—Trails to the Douglas fir tree varied over the years. Workers marked on the trunk in 1993 were observed on or near five mounds 4.0–15.1 m away. In 1994, 17 mounds, 3.8–53.6 m away (mean = 15.3 m), were connected to the Douglas fir by nine trails. Four of these trails led to single mounds, four led to two mounds, and one trail went to four mounds and branched to a fifth mound. Ants marked on the most distant mound from the tree, #70, were found on 24 other mounds up to 77.9 m away (mound O) (Fig 1).

In 1996, ten trails led to the Douglas fir from 17 mounds 4.1–52.6 m away (mean = 15.7 m). Six trails went to single mounds, three led to two mounds, and one trail led to five mounds. Six 1994 mounds (#68, 70, 94, J, M, O) no longer had trails to the tree, but six different mounds did. The longest trail came from a mound (#65) 52.6 m away that passed through two unidentified mounds and two old mounds (#84, #48) on its way to the tree (Fig 1). Ants marked on mound #65 were subsequently found on four mounds; three with trails leading to the tree.

Every year ants went into thatch at the base of the Douglas fir tree and onto the branches to tend aphids. Some workers coming down the trunk had swollen gasters and one was carrying an aphid. Ants collected insects on the tree: one was observed pursuing a small beetle and others carried small flies. Ants died while foraging; over a 20 minute period, six ants were seen carrying dead co-workers or their remains on the trunk. A number of dead ants were also found mired in tree resin.

Foraging on Plants.—Workers were observed on 12 plants in the area from late June to October: quaking aspen, Douglas fir, Rocky Mountain penstemon, silvery lupine, rubber rabbitbrush, big sagebrush, Saskatoon serviceberry, mountain snowberry, stinging nettles, Woods rose, russian thistle, and redroot buckwheat.

Ants tended aphids on nine of these plants (Table 1), but were seen most commonly on big sagebrushes which were heavily infested with aphids and visited by large numbers of ants. Some aphid locations were unusual. One aphid site was inside a curled leaf gall produced by Eriophyid mites on a quaking aspen. Large numbers of aphids were also in leaf clusters on Saskatoon serviceberry (Table 2) and mountain snowberry (Table 3). Mountain snowberry leaf clusters were 2–3 cm in diameter and one bush had at least eight leaf clusters.

Workers also tended other insects, such as psylloidea on Saskatoon serviceberry, treehoppers on rubber rabbitbrush and stinging nettles, scale insects on rubber rabbitbrush and big sagebrush, dipteran galls on big sagebrush, and mealybugs on big sagebrush and stinging nettles (Table 1).

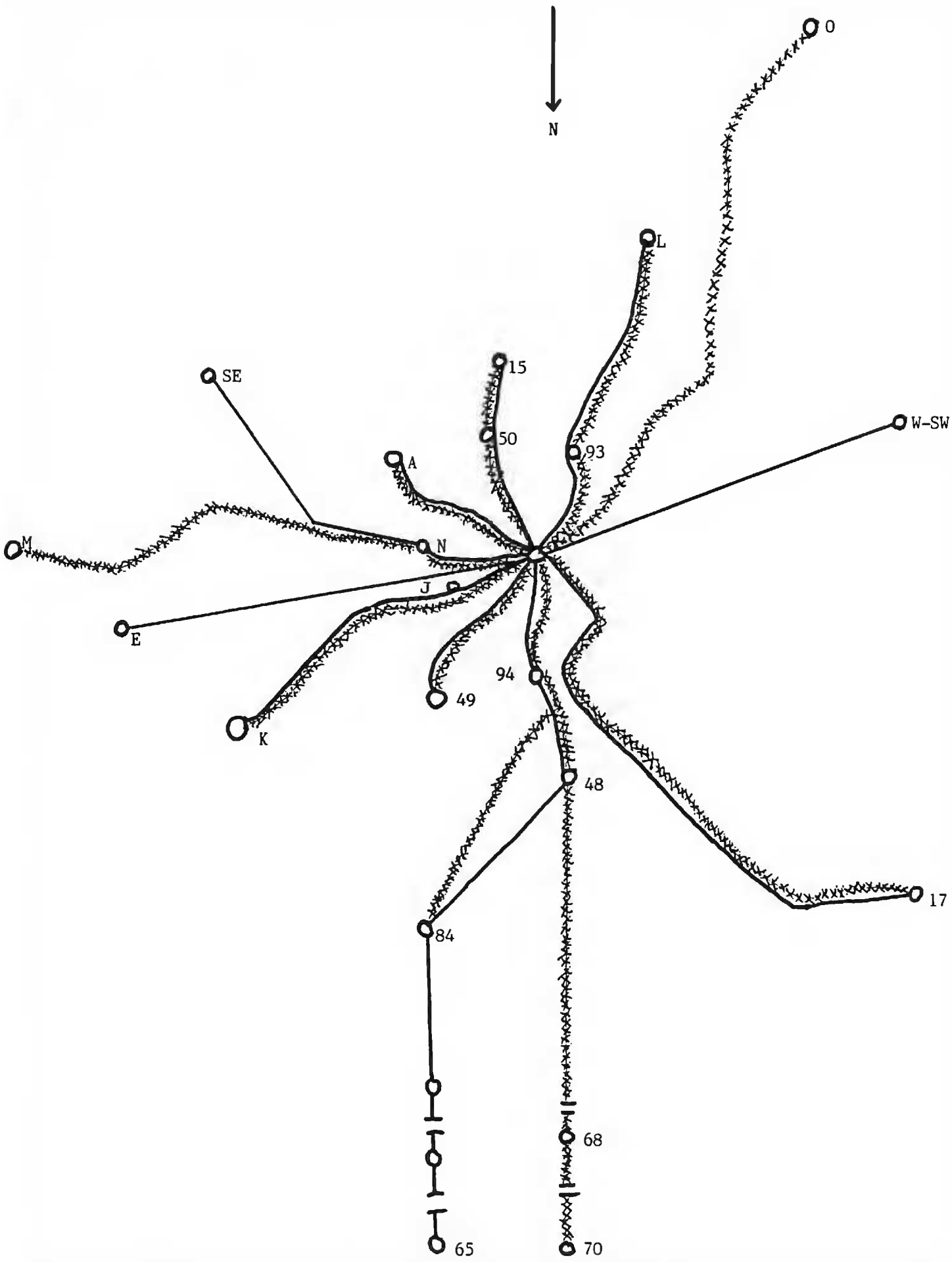

Figure 1. Trails from *Formica obscuripes* mounds to a Douglas fir tree in the summers of 1994 and 1996 at Soap Creek, Colorado study site. xxxx 1994 trails, —— 1996 trails, Scale: 1 cm = 2.2 m.

DISCUSSION

Carrion feeding appears rare in this species. Colorado ants fed on a small owl carcass and Weber (1935) reported ants feeding on Richardson ground squirrel carcasses, *Citellus richardsonii* (Sabine), placed on a mound.

Ants carried a variety of arthropods back to nests in Colorado as noted by others (Cole 1932; Weber 1935; Bradley 1973a, 1973b; O'Neill 1988; McIver & Steen 1994). Beetles were common prey in Colorado, but others reported the most common prey to be orthopterans (Weber 1935) or terrestrial isopods, leafhoppers, lepidopteran larvae and ants (O'Neill 1988). O'Neill (1988) noted ants bringing back living arthropods as I observed.

Colorado ants brought dead and live aphids to their mounds. Seibert (1992) also noted ants commonly carried dead aphids to their colonies, but Weber (1935) reported no aphids were taken to the nests.

Workers were observed with plant material at three Colorado mounds, but were not seen carrying seeds into mounds as reported by Cole (1932). Nor were yucca seeds found in the thatch and refuse piles as noted by Windsor (1964). Weber (1935) found no evidence of ants using plants as food.

Bradley (1973b) reported bear excavation of mounds as observed in this study. Other predators that have been recorded are kingbirds (*Tyrannus tyrannus* (L.) and *T. verticalis* Say), flickers (*Colaptes auratus borealis* Ridgw.), the common crow (*Corvus brachyrhynchos* Brehm), toads (*Bufo hemiophrys* Cope and *B. woodhousei* Girard) (Weber 1935), and six species of spiders (McIver & Loomis 1993).

Colorado mounds had one to five trails. Some trails branched and some trails changed during the season and from year to year as noted by O'Neill (1988).

The longest trails, 44.8 m (between mounds) and 53.6 m (between a mound and a plant), went farther than those (1–21.5 m) reported by Weber (1935), Herbers (1977), Henderson & Akre (1986), and McIver & Loomis (1993), but were shorter than the 135 m trail connecting nests reported by O'Neill (1988). The ten trails to the Douglas fir tree from 17 different mounds were greater than previously reported to a plant.

Henderson & Akre (1986) and O'Neill (1988) found that trails from several mounds frequently overlapped. O'Neill (1988) reported a system of two long parallel trails and branches serving 23 nests. In general, this did not occur in Colorado, except for some trails to the Douglas fir tree. One such trail connected five mounds.

Colonies are known to be polydomous and to reproduce by budding. I found small secondary mounds around plants along the trails from large primary mounds as noted by Herbers (1979b). Secondary mounds may become a new primary nest, serve as a refuge for aphids and ant tenders from summer heat and/or radiation, or provide a place where tenders transfer honeydew to larger ants for transport back to the primary nest (Weber 1935, Seibert 1992, McIver & Steen 1994). Henderson & Akre (1986) saw one colony relocate to a new nest site (presumably a secondary mound) 1 meter away over a period of about two weeks. They also found a secondary mound 20 m from the primary nest, which is about 5 m farther than the ones I located in Colorado.

Although Colorado workers generally followed the same trail each day as reported by Herbers (1977), marked ants were sometimes found off trails and on different trails. The maximum distance traveled by a marked worker between mounds was 77.9 m, farther than the 47.6 m reported by Weber (1935), but less than the 135 m of O'Neill (1988). I recovered ants marked on a single mound

Table 1. Insects and growths tended by *Formica obscuripes* on plants at Soap Creek, Colorado study site (*) compared to reports in literature.

Aphids (Homoptera—F. Aphididae)		
Big sagebrush—*Artemisia tridentata* Nutt		
Pleotrichophorus pseudoglandulosus (Palmer)		
Aphis sp.	*	
Aphis artemisicola Will.		
Aphis hermistonii Wil.		
Aphis oregonensis Wil.		
Macrosiphum frigidae Oest.		Jones (1929)
Aphis spp.		
Aphis minuta		
Macrosiphum spp.		Knowlton (1975)
Unident. spp.		McIver & Loomis (1993); McIver & Steen (1994)
Quaking aspen—*Populus tremuloides* Michaux		
Unidentified spp.		
Pterocomma populifoliae (Fitch)	*	
Chaitophorus sp.		
Chaitophorus populicola Thos.		Jones (1929)
Neothasmia populicola (Thos.)		Weber (1935)
Lupine—*Lupinus argenteus* Pursh		
Aphis lupini Gillette & Palmer	*	
Mountain snowberry—*Symphoricarpos rotundifolius* Gray		
Unident. spp.		
Cedoaphis incognita Hottes & Frison		
Brevicoryne symphoricarpi (Thomas)	*	
Saskatoon serviceberry—*Amelanchier alnifolia* var. *pumila*		
Unident. spp.		
Aphis sp.		
Nearctaphis sensoriata (Gillette & Bragg)	*	
Stinging nettles—*Urtica gracilis* Aiton		
Unident. spp.		
Aphis sp.	*	
Woods rose—*Rosa woodsii* Lindley		
Maculolachnus submacula (Walker)		
Unident. spp.—F. Aphididae (probable)	*	
Douglas-fir—*Pseudotsuga* sp.		
Cinara pseudotaxifoliae Palmer	*	
Lachnus splendens Gill. & Pal. on *P. taxifolia* (Poir.)		Jones (1929)
Rubber rabbitbrush—*Chrysothamnus nauseosus* (Pallas) Britton		
Unident. spp.	*	
Psylloidea (Homoptera—F. Triozidae)		
Saskatoon serviceberry—*Amelanchier alnifolia* var. *pumila*		
Probable *Trioza* sp.	*	

Table 1. Continued.

Treehoppers (Homoptera—F. Membracidae)	
Rubber rabbitbrush—*Chrysothamnus nauseosus* (Pallas)	
Publilia modesta Uhler—nymphs and adults	*
Unident. spp.	McIver & Loomis (1993); McIver & Steen (1994)
Stinging nettles—*Urtica gracilis* Aiton	
Unident. spp.	*
Scale insects (Homoptera—F. Coccidae)	
Rubber rabbitbrush—*Chrysothamnus nauseous* (Pallas)	
Unident. spp.	*
Big sagebrush—*Artemisia tridentata* Nutt	
Parthenolecanium sp.	*
Mealybugs (Homoptera—F. Pseudococcidae)	
Big sagebrush—*Artemisia tridentata* Nutt	
Amonosterium lichtensioides (Cockerell)	*
Stinging nettles—*Urtica gracilis* Aiton	
Unident. spp.	*
Dipteran galls—(Diptera—F. Cecidomyiidae)	
Big sagebrush—*Artemisia tridentata* Nutt	
Rhopalomyia pomum Gagne	*
Two unidentified growths (one containing aphids and other insects)	
Rubber rabbitbrush—*Chrysothamnus nauseosus* (Pallas)	*

on as many as 24 surrounding mounds. O'Neill (1988) found ants from eight nests on 29 other nests.

Colorado trail and mound activity varied during the day. Activity at trail checkpoints varied from 0–171 ants/minute; the latter being the highest rate reported for this species. Activity was generally high in the morning and later in the afternoon and decreased from 10:12–17:05 h, a somewhat longer duration than the 11:00–15:00 h reported by Weber (1935). As he noted, high temperatures and direct sunlight probably curtail summer midday activity. The greatest Colorado trail activity was from 17:17–18:07 h at three checkpoints; a fourth checkpoint had the greatest activity in the morning as reported by Weber (1935). Henderson & Akre (1986) noted a different circadian pattern; fairly constant foraging from 05:00–23:00 h, but little activity from 23:00–05:00 h.

I observed ants on 12 plant species and tending aphids on nine of them. Gregg (1963) also reported aphid-tending on a variety of Colorado plants. Jones (1929) listed 9 genera and 31 species of aphids on 22 plant genera in Colorado, but many of the plants and aphids differed from the ones in our study.

Colorado ants tended aphids, *Aphis* sp. and *Pleotrichophorus pseudoglandulosus* (Palmer), on big sagebrush. Although others observed ants on sagebrush (Cole 1932, Weber 1935, McIver & Steen 1994) and tending *Aphis* spp. (Jones 1929, Knowlton 1975), different aphids were also reported, such as *Macrosiphum*

Table 2. Four Saskatoon Serviceberry (*Amelanchier alnifolia* var. *pumila*) leaf clusters tended by *Formica obscuripes* at Soap Creek, Colorado study site (2560 m).

Cluster 1:	10 leaves 24 workers 403 wingless aphids (Homoptera) F. Aphididae Unidentified immature specimens *Nearctaphis sensoriata* (Gillette & Bragg) Ladybird larvae (Coleoptera) F. Coccinellidae Small wasp (Hymenoptera) F. Charipidae *Lytoxysta brevipalpis* Kieffer Parasitic hymenopteran larva Dipteran larvae (Diptera) F. Chamaemyiidae
Cluster 2:	7 leaves and 12 berries 7 workers 24 aphids (Homoptera) F. Aphididae Unidentified immature specimens F. Triozidae Probable *Trioza* sp.
Cluster 3:	8 leaves 5 workers 63 wingless aphids (Homoptera) F. Aphididae Unidentified immature specimens *Nearctaphis sensoriata* (Gillette & Bragg) 1 ladybird larva (Coleoptera) F. Coccinellidae *Scymnus* sp.
Cluster 4:	8 leaves + 4 buds 5 workers 190 aphids (1 winged) Dipteran larvae (Diptera) F. Cecidomyiidae Unidentified larvae *Bremia* sp.

spp. (Jones 1929, Knowlton 1975) (Table 1) and *Bipersona* sp. (on an unidentified sagebrush species) (Weber 1935).

I saw ants tending the aphid, *Pterocomma populifoliae* (Fitch) on quaking aspen in Colorado, but others reported species in the genera *Chaitophorus* (Jones 1929) and *Neothasmia* (Weber 1935) (Table 1).

Colorado ants tended the aphid, *Cinara pseudotaxifoliae* Palmer, on Douglas fir, but Jones (1929) reported *Lachnus splendens* Gillette & Palmer on *Pseudotsuga taxifolia* (Poiret) (Table 1).

Colorado ants tended aphids on plants not reported in the literature, such as silvery lupine, stinging nettle, Saskatoon serviceberry, mountain snowberry and

Table 3. Three Mountain snowberry (*Symphoricarpos rotundifolius* Gray) leaf clusters tended by *Formica obscuripes* at Soap Creek, Colorado study site (2560 m).

Cluster 1:	93 leaves 11 workers 1163 aphids (50 winged) (Homoptera) F. Aphididae Unidentified immatures *Cedoaphis incognita* Hottes & Frison *Brevicoryne symphoricarpi* (Thomas) Thrips (2 adults and larvae) (Thysanoptera) F. Thripidae 1st instar larva *Frankliniella occidentalis* (Perande) adults *Frankliniella* sp. larva Ladybird larvae (Coleoptera) F. Coccinellidae Dipteran larvae (Diptera) F. Chamaemyiidae and possible F. Chamaemyiidae F. Cecidomyiidae *Lestodiplosis* sp.
Cluster 2:	84 leaves 40 workers 707 aphids (28 winged) (Homoptera) F. Aphididae Unidentified immatures *Cedoaphis incognita* Hottes & Frison adults Ladybird larvae (Coleoptera) F. Coccinellidae *Scymnus* sp. Dipteran larvae and pupae (Diptera) F. Chamaemyiidae—pupae; poss. larvae F. Cecidomyiidae *Lestodiplosis* sp.
Cluster 3:	101 leaves 9 workers 906 aphids (36 winged) (Homoptera) F. Aphididae Unidentified immatures *Cedoaphis incognita* Hottes & Frison Ladybird larvae (Coleoptera) F. Coccinellidae *Scymnus* sp. Small wasp (Hymenoptera) F. Figitidae or F. Charipidae Dipteran larvae (Diptera) F. Cecidomyiidae *Lestodiplosis* sp. F. Syrphidae Syrphinae

Woods rose. McIver & Loomis (1993) and McIver & Steen (1994) reported workers foraging for honeydew on different lupine species (*Lupinus caudatus* Kellogg), but the insect was not identified.

Others noted ants tending aphids on the same genera as the Woods rose (*Rosa*) and mountain snowberry (*Symphoricarpos*) in Colorado (Weber 1935). Wheeler & Wheeler (1986) even noted the same two species of aphids on another species of *Symphoricarpos* that were on mountain snowberry in Colorado.

Knowlton (1975) reported the same aphid genus, *Pleotrichophorus* sp., on *Chrysothamnus*, that I found on big sagebrush in Colorado. This is not surprising, as it is known that one ant species may tend the same aphid species on different host plants (Jones 1929).

A new finding in Colorado was the large numbers of aphids (up to 1163) and other insects in Saskatoon serviceberry and mountain snowberry leaf clusters (Tables 2 and 3). Aphids have been reported to cause leaves to curl and have been found under curled leaves (Jones 1929, Weber 1935), but it is unclear if leaf cluster formation is due to aphid or ant activity.

The role of other insects in Colorado leaf clusters, such as a psylloidea, small wasps (F. Charipidae and possible F. Figitidae), and a parasitic hymenopteran larva are unclear. Dipteran larvae (F. Chamaemyiidae, F. Cecidomyiidae, F. Syrphidae), ladybird larvae (F. Coccinellidae), and thrip larvae and adults (F. Thripidae) in the clusters probably preyed on aphids (Tables 2 and 3). Jones (1929) suggested that ants may protect aphids from many natural enemies, such as chalcids, syrphids, coccinellids and chrysopids.

Workers tended treehopper nymphs and adults of *Publilia modesta* Uhler on rubber rabbitbrush in Colorado. Others have also noted ants tending Membracids (Wheeler 1910, Cole 1932) and collecting honeydew on rubber rabbitbrush (McIver & Loomis 1993, McIver & Steen 1994) (Table 1). O'Neill (1988) reported the membracids, *Campylenchia latipes* Say and *Publilia modesta* (Uhler), being tended on Canada thistle (*Cirsium arvense*) and chokecherry (*Prunus virginiana*).

Colorado ants also tended scale insects on rubber rabbitbrush and big sagebrush, dipteran leaf galls on big sagebrush, mealybugs on big sagebrush and stinging nettles, and two unidentified growths on rubber rabbitbrush (one housing aphids and other insects) (Table 1). They probably collected honeydew from all the above, except the dipteran galls. Further research is needed to determine if they harvest emerging flies from the latter.

Thus, as Seibert (1992) noted, *F. obscuripes* is not dependent on any one mutualistic partner. It has many nectar sources including coccids (Bradley 1973a, Seibert 1989, McIver & Steen 1994) and extrafloral nectar (Tilman 1978, Inouye & Taylor 1979, Seibert 1989).

Acknowledgment

Support for this research was provided by grants in 1993–1994 from the Howard Hughes Medical Institute through the Undergraduate Biological Sciences Education Program to the following University of Scranton students: John Bridge, Tom Sabalaske, Anthony Musingo, and Jeanne Rohan. I thank the Systematic Entomology Laboratory in Beltsville, Maryland and John T. Sorensen, Insect Taxonomy Laboratory, California Department of Food & Agriculture, Sacramento,

California for identification of insect specimens. The Forest Service in Gunnison, Colorado identified plants.

Literature Cited

Bradley, G. A. 1972. Transplanting *Formica obscuripes* and *Dolichoderus taschenbergi* (Hymenoptera: Formicidae) colonies in Jack Pine stands of southeastern Manitoba. Can. Ent., 104: 245–249.

Bradley, G. A. 1973a. Effect of *Formica obscuripes* (Hymenoptera: Formicidae) on the predator-prey relationship between *Hyperaspis congressis* (Coleoptera: Coccinellidae) and *Toumeyella numismaticum* (Homoptera: Coccidae). Can. Ent., 105: 1113–1118.

Bradley, G. A. 1973b. Interference between nest populations of *Formica obscuripes* and *Dolichoderus taschenbergi* (Hymenoptera: Formicidae). Can. Ent., 105: 1525–1528.

Clark, W. H. & P. L. Comanor. 1972. Flights of the western thatching ant, *Formica obscuripes* Forel, in Nevada. Great Basin Nat., 32: 202–207.

Cole, A. C., Jr. 1932. The thatching ant, *Formica obscuripes* Forel. Psyche, 39:30–33.

Conway, J. R. 1996. Nuptial, pre-, and postnuptial activity of the thatching ant, *Formica obscuripes* Forel, in Colorado. Great Basin Nat., 56: 54–58.

Gregg, R. E. 1963. The ants of Colorado. University of Colorado Press. Boulder, Colorado.

Henderson, G. & R. D. Akre. 1986. Biology of the myrmecophilous cricket, *Myrmecophilia manni* (Orthoptera: Gryllidae). J. Kans. Ent. Soc., 59: 454–467.

Herbers, J. M. 1977. Behavioral constancy in *Formica obscuripes*. Ann. Ent. Soc. Am., 70: 485–486.

Herbers, J. M. 1978. Trends in sex ratios of the reproductive broods of *Formica obscuripes*. Ann. Ent. Soc. Am., 71: 791–793.

Herbers, J. M. 1979a. Caste-biased polyethism in a mound-building ant species. Amer. Midl. Nat., 101: 69–75.

Herbers, J. M. 1979b. The evolution of sex-ratio strategies in hymenopteran societies. Amer. Nat., 114: 818–834.

Inouye, D. W. & O. R. Taylor. 1979. A temperate region plant-ant-seed predator system: consequences of extra floral nectar secretion by *Helianthella quinquenervis*. Ecology, 60: 1–7.

Jones, C. R. 1929. Ants and their relation to aphids. Bull. Colo. Agr. Exp. Sta., 341: 1–96.

Kannowski, P. B. 1963. The flight activities of formicine ants. Symp. Genet. Biol. Ital., 12: 74–102.

King, R. L. & R. M. Sallee. 1953. On the duration of nests of *Formica obscuripes* Forel. Proc. Iowa Acad. Sci., 60: 656–659.

King, R. L. & R. M. Sallee. 1956. On the half-life of nests of *Formica obscuripes* Forel. Proc. Iowa Acad. Sci., 63: 721–723.

Knowlton, G. F. 1975. Ants of Curlew Valley, Utah and Idaho. Utah State University Ecology Center. Terrestrial Arthropod Series No. 13: 1–10.

McCook, H. C. 1884. The rufous or thatching ant of Dakota and Colorado. Proc. Acad. Nat. Sci. Phila. Part 1: 57–65.

McIver, J. D. & C. Loomis. 1993. A size-distance relation in Homoptera-tending thatch ants (*Formica obscuripes*, *Formica planipilis*). Insect. Soc., 40: 207–218.

McIver, J. D. & T. Steen. 1994. Use of a secondary nest in great basin desert thatch ants (*Formica obscuripes* Forel). Great Basin Nat., 54: 359–365.

O'Neill, K. M. 1988. Trail patterns and movement of workers among nests in the ant *Formica obscuripes* (Hymenoptera: Formicidae). Psyche, 95: 1–13.

Seibert, T. F. 1989. Foraging on insect mutualists by the thatching ant *Formica obscuripes*: interspecific and intraspecific mechanisms and implications. Ph.D. dissertation, University of Illinois, Urbana.

Seibert, T. F. 1992. Mutualistic interactions of the aphid *Lachnus allegheniensis* (Homoptera: Aphididae) and its tending ant *Formica obscuripes* (Hymenoptera: Formicidae). Ann. Ent. Soc. Am., 85: 173–178.

Talbot, M. 1959. Flight activities of two species of ants of the genus *Formica*. Amer. Midl. Nat., 61: 124–132.

Talbot, M. 1972. Flights and swarms of the ant *Formica obscuripes* Forel. J. Kans. Ent. Soc., 45: 254–258.

Tilman, D. 1978. Cherries, ants and tent caterpillars: timing of nectar production in relation to susceptibility of caterpillars to ant predation. Ecology, 59: 686–692.

Weber, N. A. 1935. The biology of the thatching ant *Formica obscuripes* Forel in North Dakota. Ecol. Monogr., 5: 165–206.
Wheeler, W. M. 1910. Ants; their structure, development and behavior. Columbia University Press.
Wheeler, G. C. & J. N. Wheeler. 1983. The ants of North Dakota. Nat. Hist. Mus. Los Ang. Cty., Los Angeles, CA.
Wheeler, G. C. & J. N. Wheeler. 1986. The ants of Nevada. Nat. Hist. Mus. Los Ang. Cty., Los Angeles, CA.
Windsor, J. K. 1964. Three Scarabaeid genera found in nests of *Formica obscuripes* Forel in Colorado. Bull. South. Calif. Acad. Sci., 63:205–209.

Received 28 Sep 1996; Accepted 17 Apr 1997.